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REORGANIZATION OF THE CERCIDEAE (FABACEAE: CAESALPINIOIDEAE)

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ABSTRACT

The tribe Cercideae is reorganized into 12 genera placed in two subtribes, Cercidinae (*Adenolobus*, *Cercis*, *Griffonia*) and Bauhiniinae (*Bauhinia*, *Barklya*, *Brenierea*, *Gigasiphon*, *Lysiphyllum*, *Phanera*, *Piliostigma*, *Schnella*, *Tylosema*). A key to the subtribes and genera is provided.

KEY WORDS: *Adenolobus*, *Barklya*, *Bauhinia*, *Brenierea*, *Cercis*, *Gigasiphon*, *Griffonia*, *Lysiphyllum*, *Phanera*, *Piliostigma*, *Schnella*, *Tylosema*

The Cercideae has been subject to much reorganization since its establishment by Bonn (1822). Recently, Wunderlin et al. (1987) recognized five genera in two subtribes: *Adenolobus* (Harvey ex Bentham & Hook. f.) Torre & Hillcoat, *Cercis* Linnaeus, and *Griffonia* Baillon in subtribe Cercidinae; *Bauhinia* Linnaeus and *Brenierea* Humbert in subtribe Bauhiniinae. Within the large genus *Bauhinia* (300–350 species), an infrageneric system was presented that recognized four subgenera, 22 sections, and 30 series.

Molecular studies in the Cercideae have revised our thinking about the classification of the tribe. Using ITS sequences of nuclear ribosomal DNA, Hao et al. (2003) concluded that extensive reorganization is warranted in the Cercideae if monophyletic groups are to be maintained. Based on molecular data, Lewis and Forest (2005) proposed that twelve genera should be recognized: *Adenolobus*, *Barklya* F. von Mueller, *Bauhinia*, *Brenierea*, *Cercis*, *Gigasiphon* Drake del Castillo, *Griffonia*, *Lasiobema* (Korthals) Miquel, *Lysiphyllum* (Bentham) de Wit, *Phanera* Loureiro, *Pilostigma* Hochstetter, and *Tylosema* (Schweinfurth) Torre & Hillcoat. Of these, seven (*Barklya*, *Gigasiphon*, *Lasiobema*, *Lysiphyllum*, *Phanera*, *Piliostigma*, and *Tylosema*) placed in synonymy of *Bauhinia* by Wunderlin et al. (1987) were reinstated by Lewis and Forest.

Studies by Sinou et al. (2009), who sequenced the plastid *trn*L-*trn*F region of 85 species of Cercideae, provide support for the recognition of most of the genera of Lewis and Forest (2005). *Adenolobus*, *Cercis*, and *Griffonia* appear in a distinct basal clade, while two major clades emerge with the other genera. One clade contains *Bauhinia* s. str., *Brenierea*, and *Piliostigma*, while the second contains *Barklya*, *Gigasiphon*, *Tylosema*, an "American *Phanera*", and a poorly resolved *Lasiobema*-*Lysiphyllum*-*Phanera* subclade. From these data and the author's personal knowledge of morphology in the tribe, the following reorganization consisting of 12 genera is proposed.

REORGANIZATION OF CERCIDEAE

Cercideae Bronn, De Formis Pl. Legum. 131. 1822. **TYPE**: *Cercis* L.

I. Subtribe **Cercidinae**

1. **Cercis** L., Sp. Pl. 374. 1753. **TYPE**: *Cercis siliquastrum* L. Lectotypified by Britton and Brown (Ill. Fl. N. U.S., ed. 2 2: 334. 1913). – 6 species; warm temperate northern hemisphere.
Siliquastrum Duhamel, Traité Arbr. Arbust. 2: 263. 1755. ≡ *Cercis* L.

2. **Adenolobus** (Harv. ex Benth. & Hook. f.) Torre & Hillc., in Exell & Mendonça, Bol. Soc. Brot., Ser. 2 29: 37. 1956. **TYPE**: *Adenolobus garipensis* (E. Mey.) Torre & Hillc. – 2 species; Africa.

3. **Griffonia** Baill., Adansonia 6: 188. 1865. **TYPE**: *Griffonia physocarpa* Baill. – 4 species; Africa.
Bandeiraea Welw. ex Benth. & Hook., Gen. Pl. 1: 577. 1865. **TYPE**: *Bandeiraea simplicifolia* (Vahl) Oliv. Lectotypified by Oliver (Fl. Trop. Africa 2: 285. 1871).

II. Subtribe **Bauhiniinae** (Benth.) Walp., Repert. Bot. Syst. 1: 847. 1842. **TYPE**: *Bauhinia* L.

4. **Bauhinia** L., Sp. Pl. 374. 1753. **TYPE**: *Bauhinia divaricata* L. – 150–160 species; North America, Mexico, Central America, West Indies, South America, Africa, Asia, Malesia.
Pauletia Cav., Icon. 5: 5. 1799. **TYPE**: *Pauletia inermis* Cav. Lectotypified by de Wit (Reinwardtia 3: 391. 1956).
Amaria S. Mutis ex Caldas, Semanario Nueva Granada 2: 25. 1810. **TYPE**: *Amaria petiolata* S. Mutis ex DC. Lectotyified by Britton and Killip (Ann. New York Acad. Sci. 35: 164. 1936).
Casparia Kunth, Ann. Sci. Nat. (Paris) 1: 85. 1824. **TYPE**: *Casparia pes-caprae* (Cav.) Kunth. Lectotypified by Britton and Rose (N. Amer. Fl. 23: 208. 1930).
Perlebia Mart., in Martius & Spix, Reise Bras. 2: 555. 1828. **TYPE**: *Perlebia bauhinioides* Mart.
Cansenia Raf., Sylva Tellur. 122. 1838. **TYPE**: *Cansenia ungulata* (L.) Raf. Lectotypified by Wunderlin (Rhodora 78: 753. 1976).
Mandarus Raf., Sylva Tellur. 122. 1838. ≡ *Bauhinia* L.
Monoteles Raf., Sylva Tellur. 122. 1838. **TYPE**: *Monoteles paradoxa* Raf.
Telestria Raf., Sylva Tellur. 122. 1838. **TYPE**: *Telestria purpurea* (L.) Raf. Lectotypified by Wunderlin (Rhodora 78: 757. 1976).
Alvesia Welw., Ann. Cons. Ultamar. (Portugal), Parte Não Off., Ser. 1 ("Apont." 1858: 587, nom. rej. vs. *Alvesia* Welw. 1869 (Lamiaceae). **TYPE**: *Alvesia bauhinioides* Welw.
Ariaria Cuervo, Prehist. Viajes 219. 1893. **TYPE**: *Ariaria superba* Cuervo.
Caspareopsis Britton & Rose, N. Amer. Fl. 23: 217. 1930. **TYPE**: *Caspareopsis monandra* (Kurz) Britton & Rose.

5. **Barklya** F. Muell., J. Proc. Linn. Soc., Bot. 3: 158. 1859. **TYPE**: *Barklya syringifolia* F. Muell. – 1 species; Australia.

6. **Brenierea** Humbert, Compt. Rend. Hebd. Séances Acad. Sci. 249: 1599. 1959. **TYPE**: *Brenieraea insignis* Humbert – 1 species; Madagascar.

7. **Gigasiphon** Drake, in Grandidier, Hist. Phys. Madagascar 30(1): 88. 1902. **TYPE**: *Gigasiphon humblotianum* (Baill.) Drake – 5 species; Africa, Malesia.
Tournaya A. Schmitz, Bull. Jard. Bot. Natl. Belg. 43: 397. 1973. **TYPE**: *Tournaya gossweileri* (Bakh. f.) A. Schmitz.

8. **Lysiphyllum** (Benth.) de Wit, Reinwardtia 3: 431. 1956. **TYPE**: *Lysiphyllum cunningamii* (Benth.) de Wit. Lectotypified by de Wit (Reinwardtia 3: 431. 1956) – 9 species; Africa, Asia, Malesia, Australia.

Bracteolanthus de Wit, Reinwardtia 3: 415. 1956. **TYPE**: *Bracteolanthus dipterus* (Blume ex Miq.) de Wit.

9. **Phanera** Lour., Fl. Cochinch. 37. 1790. **TYPE**: *Phanera coccinea* Lour. – Ca. 90-100 species; Asia, Malesia.

Lasiobema (Korth.) Miq., Fl. Ned. Ind. 1(1): 71. 1855. **TYPE**: *Lasiobema scandens* (L.) de Wit. Lectotypified by de Wit (Reinwartia 3: 422. 1956).

10. **Piliostigma** Hochst., Flora 29: 598. 1846, nom. cons. **TYPE**: *Piliostigma reticulatum* (A. DC.) Hochst., type cons. – 5 species; South America, Africa, Asia, Malasia, Australia.

Elayuna Raf. Sylva Tellur. 145. 1838, nom. rej. vs. *Piliostigma* Hochst. **TYPE**: *Elayuna biloba* Raf.

Locellaria Welw., Ann. Cons. Ultamar. (Portugal), Parte Não Off., Ser. 1 ("Apont.") 1858: 588. **TYPE**: *Locellaria bauhinioides* Welw.

11. **Schnella** Raddi, Quar. Piant. Nuov. Bras. 32. 1820. **TYPE**: *Schnella macrostachya* Raddi. Lectotypified by Britton and Rose (N. Amer. Fl. 23: 205. 1930). – Ca. 40 species; Mexico, Central America, South America.

Lacara Spreng., Neue Entdeck. Pflanzenk. 3: 56. 1822. **TYPE**: *Lacara triplinervia* Spreng.

Caulotretus Rich. ex Schott, in Sprengel, Syst. Veg. 4(2): 406. 1827. **TYPE**: *Caulotretus smilacinus* Schott.

12. **Tylosema** (Schweinf.) Torre & Hillc., in Exell & Mendonça, Bol. Soc. Brot., ser. 2. 29: 38. 1955. **TYPE**: *Tylosema fassoglensis* (Kotschy ex Schweinf.) Torre & Hillc. – 4 species; Africa.

KEY TO THE SUBTRIBES AND GENERA OF THE CERCIDEAE

1. Seeds with a circular hilum; funicular aril lobes absent (**I. Subtribe Cercidinae**).

2. Fruits with a dorsal wing; corolla pseudopapilionaceous; temperate northern hemisphere ..... ***Cercis***

2. Fruits lacking a dorsal wing; corolla only slightly zygomorphic; Africa.

3. Gynophore free from the abaxial wall of the hypanthium; fruit with the gynophore and persistent style appearing confluent with the dorsal margin (semilunate), valves thin; shrubs or small trees ..... ***Adenolobus***

3. Gynophore connate with the abaxial wall of the hypanthium; fruit with the gynophore and persistent style obliquely attached, valves thick; scandent shrubs or lianas ..... ***Griffonia***

1. Seeds with a crescentic hilum; funicular aril lobes present (**II. Subtribe Bauhiniinae**).

4. Branches modified into cladodes; petals absent ..... ***Brenierea***

4. Branches not modified into cladodes; petals (1–)5(–6).

5. Trees or shrubs (rarely semiscandent), sometimes with intrastipular spines, rarely with thorns, never with tendrils.

6. Calyx spathaceous or dividing to the hypanthium into 2–5 lobes.

7. Leaves entire, the midrib stout and with strong lateral veins; sepals with an apical nectary ..... ***Gigasiphon***
7. Leaves entire, bilobed, or entire (if entire, the midrib lacking strong lateral veins); sepals lacking an apical nectary ..... ***Bauhinia***

6. Calyx only lobed in the upper part.

8. Calyx closed and irregularly splitting at anthesis ..... ***Piliostigma***
8. Calyx open before anthesis ..... ***Barklya***

5. Lianas, or vines (rarely shrubs) with tendrils (rarely without), never with intrastipular spines or thorns.

9. Fertile stamens 10.

10. Calyx regularly split in the upper part or to the mouth of the hypanthium into 2–5 lobes; Africa, Asia, Malesia, and Australia ..... ***Lysiphyllum***
10. Calyx irregularly 2- to 5-lobed or dentate in the upper part; tropical North and South America ..... ***Schnella***

9. Fertile stamens 2–3.

11. Fertile stamens 2; upper petal smaller and bicallose at the base ..... ***Tylosema***
11. Fertile stamens 3; upper petal larger, not bicallose at the base ..... ***Phanera***

DISCUSSION

A diagram of subtribal and generic relationships in the Cercideae presented here (Fig. 1) includes two subtribes and 12 genera. It incorporates molecular (Forest unpublished, cf. Lewis & Forest 2005; Sinou et al. 2009;) and morphological data from a variety of sources, including recent monographs, revisions, floras, and the author's personal study of the tribe during the last 30 years. This system is similar to that of Lewis and Forest (2005) except that *Schnella* is recognized as a genus distinct from *Phanera* and the genus *Lasiobema*, recognized by Lewis and Forest (2005), is placed in synonymy in *Phanera*.

Figure 1 shows subtribe Cercidinae with the warm temperate genus *Cercis* as basal and a clade containing the African genera *Griffonia* and *Adenolobus* as sister to *Cercis*. The placement of these three small distinctive genera, as proposed by Wunderlin (1987), remains unchanged.

Bauhiniinae has two major clades containing the remaining nine genera. The first has the large pantropical *Bauhinia* (150–160 species), and the two small genera *Brenierea* (1 species; Madagascar) and *Piliostigma* (5 species; 3 in the tropical Old World, 2 in South America). With the exception of the very distinctive *Brenierea*, all were previously recognized by Wunderlin (1987) as sections of *Bauhinia*. The second clade contains the three small genera, *Barklya* (1 species; Australia), *Gigasiphon* (5 species; Africa, Malesia), and *Tylosema* (4 species; Africa) and three closely related genera, *Lysiphyllum* (9 species; Old World tropics), *Phanera* (90–100 species; Asia, Malesia), and *Schnella* (ca. 40 species; tropical America). All of these were previously recognized by Wunderlin (1987) within *Bauhinia*. *Lasiobema*, recognized at the generic level by Lewis and Forest (2005) who alluded to the fact that it is not well supported by molecular data, is here included with *Phanera*. Morphological data also does not support its segregation from *Phanera*. *Lysiphyllum* is sister to *Phanera* (Fig. 1) and is readily distinguished from that genus by having 10 fertile stamens

(*Phanera* having 2–3 fertile stamens) (see key). Preliminary molecular data (Forest unpubl., cf. Lewis & Forest 2005; Sinou 2009) show *Schnella* as distinct from *Phanera*. This is supported by morphological data and *Schnella* is accordingly elevated to the genus level here. The neotropical genus *Schnella* is very distinctive from the paleotropical genus *Phanera* and can easily be distinguished by its species having 10 fertile stamens (vs. 2–3 fertile stamens in *Phanera*).

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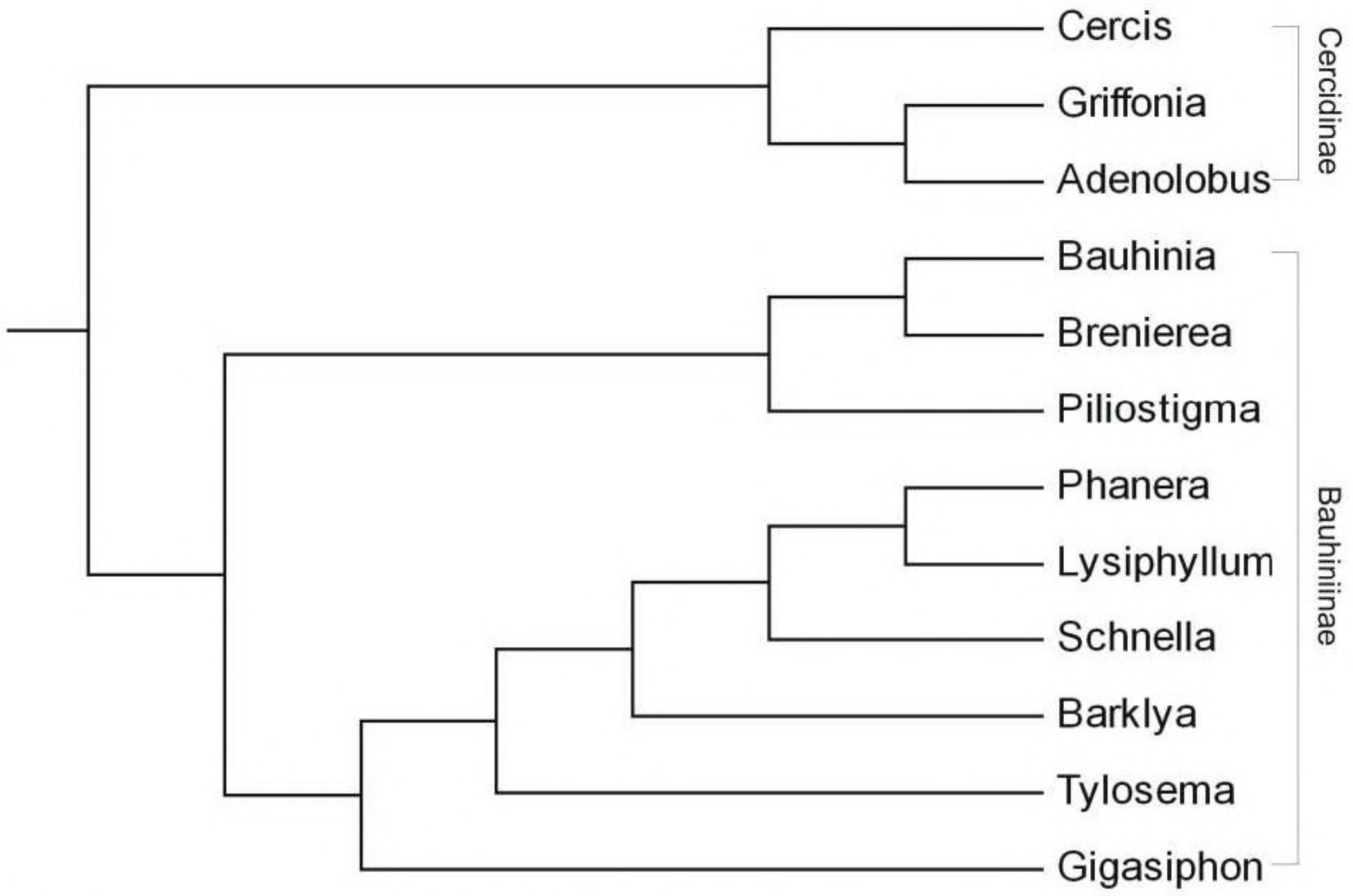

Figure 1. Diagram of relationships in the tribe Cercideae.